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Decomposition of leaf litter in a mull beech forest: comparison between canopy and herbaceous species

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Summary. Patterns of decomposition of leaf litter of canopy and understory herbaceous species were compared in the Göttinger Wald, a beech forest on mull soil. Impacts of the meso- and macrofauna on rates of litter disappearance and changes in C and N content of the litter during decomposition were determined by exposing the litter in bags of 45 µm, 1 mm and 3.5 mm mesh for up to 1.4 years. Litter of both herbaceous species (*Anemone nemorosa* and *Mercurialis perennis*) decomposed rapidly. Half of the litter had disappeared within 48 days from the 45 µm bags (the treatment that excluded the fauna). Both meso- and macrofauna accelerated decomposition of herb litter. Within 10 days, 50% had disappeared from the 3.5 mm bags (the treatment that permitted access to both meso- and macrofauna). Litter of canopy species decomposed more slowly. Fifty percent of a mixture of ash (*Fraxinus excelsior*) and maple (*Acer* spp.) litter had disappeared within 280 and 60 days from the 45-µm and 3.5-mm mesh bags, respectively. Freshly fallen leaves of beech (*Fagus sylvatica*) and year-old beech litter decomposed much more slowly than litter of herbs or ash-maple. Over 50% of both categories of beech litter remained after 1.4 years, even in the 3.5-mm mesh bags. The fauna had no significant impact on the rate of disappearance of fresh beech leaves, and only the macrofauna accelerated the disappearance of aged beech.
Nitrogen content increased, and the C N ratio decreased, of all categories of litter in the 45-µm mesh bags. The impact of the fauna on nutrient content of each litter category tended to mirror the extent to which the fauna fed on that category. Feeding by the fauna on herbs, ash, maple and aged beech retarded or prevented the increase in N content. This pattern suggests that nitrogen content influenced palatability of the litter to the fauna, although the correlation coefficient between initial nitrogen content and the decomposition coefficient [k (yr^{-1})] was not statistically significant ($r = 0.63$, df = 3; 3.5-mm mesh bags). Our findings support the hypothesis that herbaceous litter plays an important role in maintaining high densities of the fauna in beech forests on mull soils. We come to this conclusion because the fauna did not attack fresh beech leaves, but readily consumed herb litter, which previous research has demonstrated comprises a substantial fraction of the litter input to the Göttinger Wald. We discuss the evidence for this hypothesis in light of contradictory evidence from several studies regarding the extent to which animals consume fresh beech litter.

Key words: Decomposition, litterbag experiment, mull beech forest, canopy leaf litter, herbaceous leaf litter, carbon/nitrogen ratio

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Introduction

The rate and temporal pattern of decomposition of leaf litter depend upon physical and chemical properties of the litter material, soil characteristics, climate, and influence of the soil biota (Swift et al. 1979). Although climatic conditions and litter quality appear to be the most important controlling factors (Meentemeyer 1978; Edwards et al. 1981; McClaugherty et al. 1985), the abundance and diversity of the soil fauna can also play a major role in determining decomposition rate. This is well illustrated by the mull-moder dichotomy of humus forms.

The macrofauna have a large impact on the decomposition process in temperate deciduous forests on mull soil (Wallwork 1976; Schaefer 1990; Schaefer & Schauermann 1990). In these forests the fauna feed upon two very different types of leaf-litter resource: leaves of canopy trees, which enter the system in an autumnal pulse; and leaves of understory herb species, which as a whole enter the system more continuously during the period of faunal activity.

It is well established that decomposer organisms more readily utilize herbaceous material because it has a higher nitrogen content and a lower content of structural polysaccharides than the leaves of canopy species (Esser 1958; Eggert 1986; Ellenberg et al. 1986; Meiwes & Beese 1988; Sah 1990). Despite clear documentation of these differences, until now no systematic studies exist comparing rates and patterns of processing of these two resource types in the same forest. Such an analysis, conducted in a forest on mull soil, would be valuable in two respects. First, observed differences in the fate of the two litter types would reflect differences in litter quality and not variation in other controlling factors, such as composition of the soil fauna, that vary between forests. Secondly, knowledge of the utilization patterns of herbaceous and canopy litter by major elements of the fauna would improve our understanding of the role that the litter of herbaceous species may play in maintaining the high macrofaunal biomasses characteristic of mull soils.

We report results of litterbag experiments in which we measured rates of disappearance of different types of leaf litter from bags of fine, medium or coarse mesh in order to address the two issues just mentioned, and also to test the following specific hypotheses: (1) litter of understory herbaceous species decomposes much faster, and is much more readily utilized by the soil fauna, than canopy leaf litter; (2) beech litter is more resistant to decomposition than the litter of other canopy species; and (3) nitrogen content of the litter influences the participation of the macrofauna in the decomposition process.

We performed the study in a mull beech forest on limestone for which the fauna is well characterized (Schaefer 1990). This forest has a high faunal biomass (about 15 g d wt m^{-2}), with earthworms being the most prominent group. Other important detritivores of the macrofauna in this forest include gastropods, isopods, diplopods and dipteran larvae (Schaefer & Schauermann 1990). Saprophages consume a large portion of the annual litter input, which is approximately 6000 kJ m^{-2} of canopy species, and 1800 kJ m^{-2} of herbaceous litter (Schaefer 1990). Our experiments demonstrate that rates of disappearance, and both the extent and patterns of utilization by the fauna, differ markedly between herbaceous and canopy litter. Our results also confirm the major contribution of the fauna to regulating the rate at which leaf litter is decomposed in this mull forest, and in addition, support the hypothesis that a continuous input of herb litter sustains high biomasses of saprophagous macrofauna in mull beech forests.

Materials and Methods

Study site

The experiments were conducted in the "Göttinger Wald", a beech forest in southern Lower Saxony (Germany) situated on a Muschelkalk plateau 420 m above sea level. The forest, which is 105 – 120 years old, has a rather uniform, dense canopy layer consisting almost exclusively of beech (*Fagus sylvatica*)

trees. A few other species are interspersed – mostly ash (*Fraxinus excelsior*) and maple species (*Acer platanoides* and *A. pseudo-platanus*), with fewer numbers of *Quercus robur*, *Q. petraea* and *Ulmus scabra*. A shrub layer is not developed, though there is a higher growth of young *Fraxinus excelsior* in gaps. The understory herb layer is, with few exceptions, dense and diverse. Dominant spring geophytes are *Anemone nemorosa* and *Allium ursinum*. Additional dominant herbs are *Mercurialis perennis*, *Asarum europaeum*, *Hordelymus europaeus*, *Galium odoratum*, *Lamiastrum galeobdolon*, *Oxalis acetosella* and *Primula elatior*. The forest belongs to the Melico-Fagetum hordelymetosum. Dierschke provides further details (1989; Dierschke & Song 1982). The soil is shallow and consists of terra fusca-rendzina (*ca.* 50%), rendzina (*ca.* 26%), terra fusca (*ca.* 14%) and some other modifications containing brown earth (Meiwes & Beese 1988). The pH ranges from 6.8 to 4.3 (Aldag, pers. comm.). During the period of this study (1985–87) estimated mean annual temperatures for the research site were 6, 6.7 and 6 °C for 1985, 1986, and 1987, respectively. Respective estimates of annual precipitation amounts were 706, 726, and 717 mm. These values compare with long-term averages of *ca.* 7 °C and 700 mm. In this forest the amount of leaf litter varies from *ca.* 450 g d wt m^{-2} in late summer to *ca.* 700 g d wt m^{-2} in winter [values for 1981 (Schaefer 1990)].

Herbaceous litter

Rates of disappearance and changes in carbon and nitrogen content were determined for representative understory species: a spring herb, *Anemone nemorosa*, and a summer herb, *Mercurialis perennis*. Bags (n = 120) containing leaves of *Anemone* were placed on the forest floor 21 June 1985 and were sampled through 20 June 1986. On five dates we removed eight each of the medium- and coarse-mesh bags. The fine-mesh treatment was sampled six times, eight or four bags each date. We employed a similar sampling design for *Mercurialis*, starting the experiment with litter of this species on 1 September 1985 and continuing through 16 July 1986.

Litterbags were arranged in eight blocks, one replicate of each treatment combination per block. The bags of *Mercurialis* were placed in the same eight areas as the *Anemone* bags. Although sampling dates were not the same for the two species, sampling intervals were similar. Thus, we have combined results of both species into one randomized block design for statistical analysis, recognizing that days of exposure from Day 0 for *Anemone* and *Mercurialis* occurred at different times of the year. However, sampling was most intensive during the first 10 weeks, which was completed for both species before winter arrived.

Litter of canopy species

We investigated decomposition of three categories of canopy litter: a 1:1 mixture of leaves of ash (*Fraxinus excelsior*) and maple spp. (equal amounts of *Acer platanoides* and *Acer pseudo-platanus*); freshly-fallen leaves of beech (*Fagus sylvatica*); and aged beech litter from underneath newly fallen leaves. Leaves were collected from the forest floor during the middle of November and bags with litter (n = 378) were placed in the field on 29 November 1985. Six replicates of each treatment were collected on seven dates through 8 April 1987.

Determination of dry weight, ash-free weight, % C and % N

Leaves to be added to the litterbags were first dried at 25 °C; sub-samples were also dried at 105 °C, weighed, and then burned in a muffled furnace at 550 °C to determine ash content. Measured amounts of the litter dried at 25 °C (*ca.* 2 g of the herbaceous species and *ca.* 3 g each of the three categories of canopy litter) were placed in 15 cm × 15 cm nylon litterbags of either fine (45 µm), medium (1 mm) or coarse (3.5 mm) mesh. The fine mesh excluded meso- and macrofauna, the medium mesh prevented macrofauna from entering, and the coarse mesh allowed access to the litter of all smaller animals and most categories of the macrofauna, including earthworms. Each bag was placed on the forest floor in contact with the soil surface, in a randomized block design. On each sampling date one replicate per treatment was collected from each block (with the exception of the fine-mesh bags, for which only four blocks were sampled on the final two dates). Litterbag contents were examined in the laboratory and macrofaunal species were removed. The leaf litter was then dried at 105 °C and weighed, and ash

content was determined. On most sampling dates another sub-sample was analyzed with a gas chromatograph (Elemental Analyzer, Fa. Carlo Erba, Milan) for carbon and nitrogen content. The amount of litter remaining in a bag is always expressed as a proportion of the initial amount [either dry weight (105 °C) or ash-free dry weight]. Carbon and nitrogen content are expressed as % of ash-free dry mass.

Statistical analyses

Three-way ANOVA (litter type × mesh size × days exposed; randomized complete block design; separate ANOVAs for herbaceous litter and canopy species) is the most straightforward technique for evaluating the extent to which litter quality and the fauna influence the overall rate, and the temporal pattern, of litter disappearance and changes in nutrient content. Log-transforming the data satisfied assumptions of ANOVA for C, N and C/N in the experiments with herbaceous litter. However, after transformation variances were highly heterogeneous for the amount of litter remaining in all experiments, and for the nutrient content of canopy litter. We employed two statistical approaches to solve the problem of heterogeneous variances:

(1) *Friedman's Test on final values:* Friedman's χ^2, a non-parametric equivalent of a randomized block one-way ANOVA, was calculated for the final values of those variables for which a full ANOVA was not possible. This procedure was used to uncover interactions indirectly by examining the statistical significance of effects of a particular treatment at each level of the other treatment.

(2) *Analysis of mean values calculated across sampling dates:* Besides lacking the interaction term of an ANOVA, approach (1) above also has drawbacks because it places considerable weight on the final value of a variable. This could present a problem of interpretation in some instances because of the small amounts of material remaining at the end of the experiment. Consequently, we also determined the mean value of each variable, calculated as the average value for all sampling dates. If variances of this response variable were homogeneous, we performed ANOVA (either one- or two-way, depending upon which design yielded homoscedastic variances). If variances were heteroscedastic, we again relied on Friedman's Test.

SAS procedures (SAS Institute 1989) were used for all statistical analyses.

Results

Rate of litter disappearance

Herbaceous and canopy litter differed markedly in the rate at which dry weight decreased. Herbaceous litter disappeared rapidly (Fig. 1). The time required for 50% of the litter to vanish was 48 days in bags with fine mesh, and 10 days in coarse-mesh bags (values interpolated from Fig. 1). Litter of canopy species disappeared much more slowly (Fig. 2). After 495 days, over 50% of both fresh and aged beech litter still remained, even in the coarse-mesh bags. The ash-maple litter disappeared more rapidly (50% had disappeared by 280 days and 60 days from fine- and coarse-mesh bags, respectively), but still more slowly than the leaf litter of unterstory herbaceous species. The difference between ash-maple and herbaceous litter is also apparent when comparing amounts remaining after a year. Such a comparison compensates in large part for the difference in timing of the two experiments. After one year over 40% of the ash-maple leaves remained in the fine-mesh treatment, and over 10% was still present in the coarse-mesh bags. In contrast, *ca.* 30% of the herbaceous litter remained in the fine-mesh bags after a year. The coarse-mesh treatment was not sampled past 70 days for the herb species; by this time only 3% of the litter remained.

Rates of disappearance differed between species within the same category. Of the two herbaceous species, *Mercurialis* vanished at a slightly faster rate. The difference is statistically significant by three criteria: (1) amount remaining after 70 days [$P(\chi^2$-Friedman's Test) < 0.05, fine mesh: $P(\chi^2) < 0.01$, coarse mesh: NS for medium mesh]; (2) two-way ANOVA

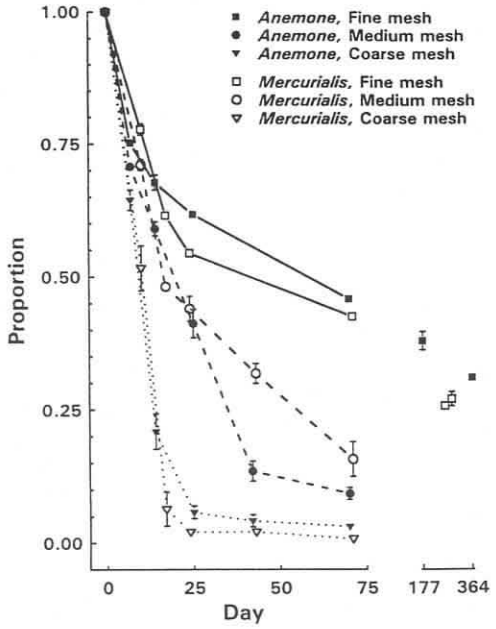

Fig. 1. Change in amount of herbaceous litter, expressed as proportion of initial dry weight, in bags of fine, medium and coarse mesh. Day 0 for *Anemone* was 21 June 1985; Day 0 for *Mercurialis* was 1 September 1985. Means ± SE. On several dates error bars are smaller than the width of the symbol

of the mean dry weight calculated over the first 10 weeks of the experiment (Table 1); and (3) amount of litter remaining in fine-mesh bags after 9 – 12 months (Fig. 1). The difference in disappearance rate among canopy species was much more marked. In all treatments the ash-maple litter vanished much faster than beech leaves (Fig. 2); and within the beech litter, freshly fallen leaves disappeared more rapidly than aged leaves, but only in the two treatments (fine and medium mesh) not affected by the fauna (results of one-way ANOVAs of the average amount of litter present over the experiment and comparisons by the Least Significant Means test).

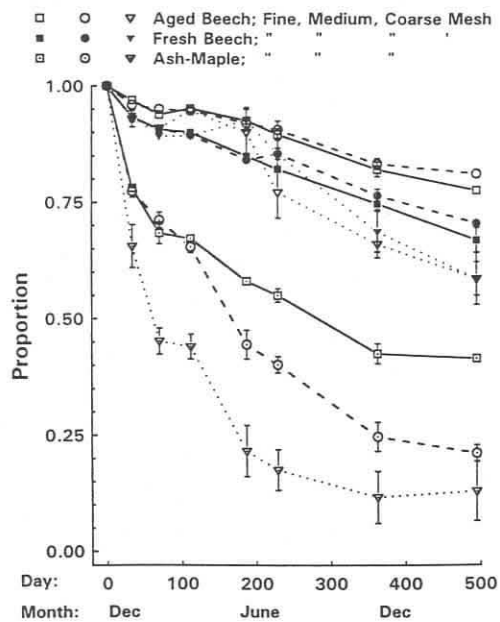

Fig. 2. Change in amount of canopy litter, expressed as proportion of initial dry weight, in bags of fine, medium and coarse mesh. Means ± SE

Table 1. Summary of two-way ANOVAs (litter type and mesh size) of mean amount of herbaceous litter present during the first ten weeks. Mean proportion of the initial dry weight that remained was calculated over the four dates on which bags of all three mesh treatments were collected (Fig. 1)

Source of variation	df	MS	*F*	*P*
Block	7	0.00051961	0.85	0.554
Litter	1	0.00704502	11.54	0.002
Mesh	2	0.80020660	1310.50	<0.001
Litter × mesh	2	0.01126460	18.45	<0.001
Error	35	0.00061061		
Total	47			

Excluding the fauna dramatically retarded the rate of disappearance of herb and two catogories of canopy litter (Figs. 1, 2). Denying access of the entire fauna to herb litter increased the amount remaining after 70 days by an order of magnitude (*ca.* 45% remained in fine-mesh bags compared to 3% for the coarse-mesh treatment). Contributions of the meso- and macrofauna are comparable as judged by differences between mesh treatments in mean amount of herbaceous litter remaining, calculated across sampling dates for the first ten weeks. Values ± SE were 61 ± 1%, 40 ± 1%, and 16 ± 1% for fine, medium and coarse meshes, respectively. All differences between mesh treatments are highly significant ($P < 0.001$), either for ANOVA of mean amounts (Table 1) or separate Friedman's tests of the amount remaining on Day 70. Excluding the fauna also affected rates of disappearance of canopy litter, but not as markedly as for *Anemone* and *Mercurialis*, and the pattern is more complicated (Table 2). Relative effects of the meso- and macrofauna on the average disappearance rates of ash-maple were similar to impacts of the fauna on herb litter, with the exception that the onset of winter affected the initial pattern. The macrofauna consumed ash-maple litter during the winter, but the mesofauna had no impact until spring. The fauna had no clear impact on the average amount of freshly fallen beech leaves, and only the macrofauna accelerated the rate at which aged beech leaves disappeared. The extent of enhancement was less than macrofaunal effects on the disappearance rates of herb or ash-maple litter.

The preceding analyses of faunal effects have the potential to be misleading for two reasons:

(1) The ash content of herbaceous and canopy litter increased over the course of the experiment (Figs. 3, 4). However, analyses by ANOVA and Friedman's Test of treatment effects on litter amounts based upon ash-free dry weights yielded results similar to those presented above for dry-weight amounts. This similarity reflects the fact that ash content of litter in all three mesh treatments increased during the experiments.

Table 2. Results of Friedman's Test of effect of mesh size on the mean amount of canopy litter present over the course of the experiment

Litter	Mesh size	Mean percentage over experiment ±SE	$P(\chi^2)$ from Friedman's Test
Ash-Maple	Fine	58.6 ± 0.6	$P = 0.002$
	Medium	49.1 ± 0.8	
	Coarse	31.8 ± 3.2	
Fresh Beech	Fine	83.3 ± 0.6	$P = 0.607$
	Medium	84.3 ± 0.2	
	Coarse	82.3 ± 2.1	
Aged Beech	Fine	89.6 ± 0.3	$P = 0.002$
	Medium	90.5 ± 0.5	
	Coarse	81.4 ± 1.6	

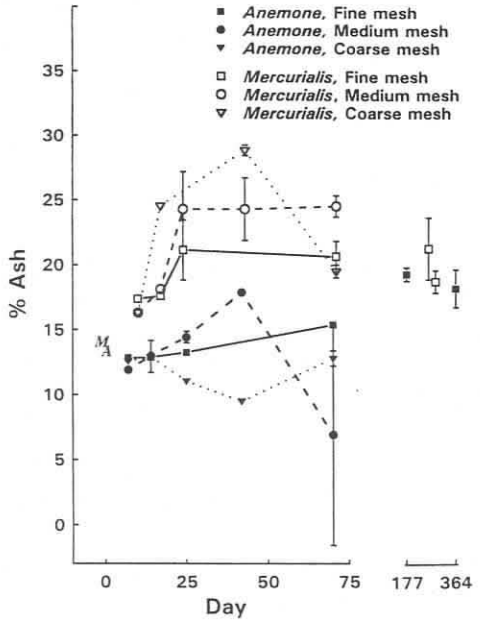

Fig. 3. Change in ash content of herbaceous species. Dates given in legend of Fig. 1. Means ± SE

(2) ANOVA of the overall average amount of litter may fail to uncover changes between treatments that develop later in the experiment. For example, it appears that the macrofauna may have slightly decreased the amount of fresh-beech litter during the last half of the experiment (Fig. 2). Examining interaction terms that include "Days of Exposure" would reveal such patterns, but heteroscedastic variances make suspect the results of such an ANOVA. One remedy is to describe the pattern of litter disappearance by a simple mathematical model and compare parameter values that reflect rates of disappearance. Because of changing influence of moisture and temperature during the year, and changing

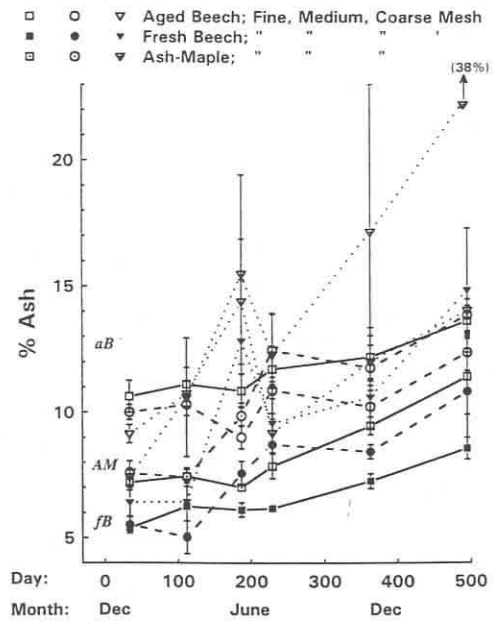

Fig. 4. Change in ash content of canopy species. Means ± SE

Table 3. Yearly decomposition rates, k (yr^{-1}), obtained by fitting litter amount to the model of simple exponential decay, $x(t) = e^{-kt}$. Rates are the slope of the linear regression of $\log_e$ *(proportion remaining)* versus *days exposed* over the first year of the experiment

Mesh size	Litter type	Change in dry wt $k \pm$ SE (yr^{-1})	Change in ash-free dry wt $k \pm$ SE (yr^{-1})
Fine	*Anemone*	1.55 ± 0.16	1.52 ± 0.14
	Mercurialis	2.03 ± 0.17	1.98 ± 0.17
	Ash-maple	0.97 ± 0.04	0.96 ± 0.03
	Fresh beech	0.31 ± 0.01	0.33 ± 0.01
	Aged beech	0.19 ± 0.01	0.17 ± 0.01
Medium	*Anemone*	13.99 ± 0.50	13.51 ± 0.51
	Mercurialis	10.58 ± 0.45	10.65 ± 0.50
	Ash-maple	1.49 ± 0.05	1.53 ± 0.05
	Fresh beech	0.29 ± 0.01	0.32 ± 0.01
	Aged beech	0.18 ± 0.09	0.14 ± 0.01
Coarse	*Anemone*	24.13 ± 1.56	23.57 ± 1.51
	Mercurialis	32.97 ± 2.52	31.05 ± 2.18
	Ash-maple	2.75 ± 0.18	2.83 ± 0.19
	Fresh beech	0.33 ± 0.03	0.40 ± 0.03
	Aged beech	0.39 ± 0.04	0.37 ± 0.04

composition of the litter, simple exponential functions often are not the most realistic descriptors of litter decomposition (Minderman 1968; Howard & Howard 1974; Wieder & Lang 1982). Nonetheless, for the patterns uncovered in our study, a one-parameter exponential model is adequate for the purposes of assessing treatment effects. Results are summarized in Table 3. Differences in k of the negative exponential model display the same pattern of effects due to litter types and faunal influences as revealed by ANOVA and Friedman's tests. Futhermore, the pattern of k values confirms that patterns of change in dry weight and ash-free weight are very similar.

Changes in C, N and C/N: herbaceous litter

Patterns of change in carbon, nitrogen and C/N ratio are basically similar for *Anemone* and *Mercurialis* (Figs. 5, 6), though some differences are apparent. Because the experiment ran the longest and variances were the smallest for the fine-mesh bags, the pattern is clearest for this treatment. In the absence of the fauna, C and N in the litter of both species increased over the span of a year. For *Anemone* the C/N ratio declined from *ca.* 30 to 14, whereas the C/N ratio of *Mercurialis* stayed relatively constant, declining rapidly from *ca.* 15 to 12. The primary cause of this difference in pattern is the initially lower N content of *Anemone* litter.

Analyzing patterns for the other mesh treatments is slightly more complicated, since on later sampling dates we had to combine samples for C/N analyses because the fauna had removed most of the litter. Small numbers of replicates on some dates make it difficult to infer patterns by simply examining changes in means and relative standard errors on the graphs. Therefore, we analyzed the pattern of change in C and N over 10 weeks of exposure by both three-way ANOVA (litter type × mesh size × days exposed), and separate two-way ANOVAs for each litter type.

Several conclusions are apparent from the three-way ANOVAs (Table 4): (1) *Anemone* and *Mercurialis* differed in average C, N and C/N; (2) N and C/N changed more consistently than C (note that $P(F)$ for "days exposed" in the three-way ANOVA of C content is not statistically significant); (3) excluding the fauna substantially affected C, N and C/N, and

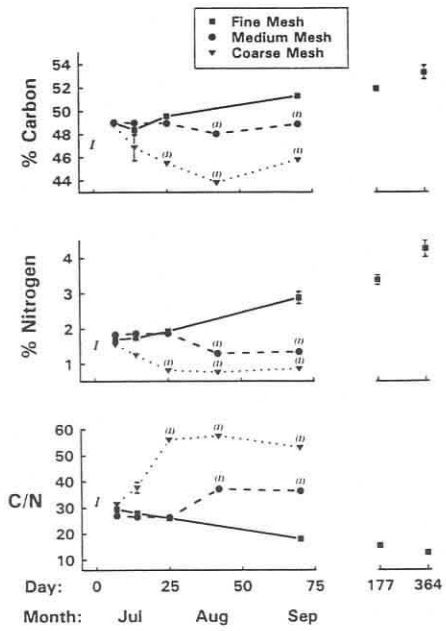

Fig. 5. Change in % C, % N, and C/N ratio of *Anemone* litter. "*I*" indicates initial value. On some dates n = 1 for medium-mesh and coarse-mesh treatments. Means ± SE

the effect increased over time: (4) there was no significant change in the difference between *Anemone* and *Mercurialis* in N and C/N over time, and the effect of excluding the fauna on N and C/N was the same for both species (unlike the situation for C content, for which the interaction terms "litter × day" and "litter × mesh" are statistically significant). Because *Anemone* and *Mercurialis* differed significantly, and because some of the interaction terms involving "litter" were significant, we also performed separate two-way ANOVAs for *Anemone* and *Mercurialis* in order to uncover temporal patterns (Table 5).

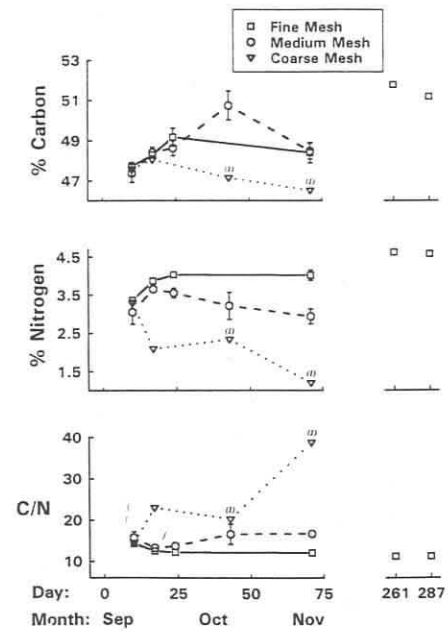

Fig. 6. Change in % C, % N and C/N ratio of *Mercurialis* litter. Initial values were not determined. On the last two sampling dates, n = 1 for coarse-mesh treatments. Means ± SE

Table 4. Summary of three-way ANOVAs (litter type, mesh size and days exposed) of nutrient content of herbaceous litter over 10 weeks of exposure. Total degrees of freedom are less than the full design because some replicates were not analyzed for nutrient content

Dependent variable	Source of variation	df	MS	*F*	*P*
Carbon	Block	7	0.00004561	1.14	0.356
	Litter	1	0.00021703	5.40	0.024
	Mesh	2	0.00097222	24.19	<0.001
	Days	3	0.00000083	0.02	0.996
	Litter × mesh	2	0.00020911	5.20	0.009
	Mesh × days	6	0.00027330	6.80	<0.001
	Litter × days	3	0.00019166	4.77	0.005
	Litter × mesh × days	5	0.00011996	2.98	0.019
	Error	52	0.00004019		
	Total	81			
Nitrogen	Block	7	0.00404463	2.23	0.046
	Litter	1	0.78029884	430.75	<0.001
	Mesh	2	0.24228309	133.75	<0.001
	Days	3	0.01969023	10.87	<0.001
	Litter × mesh	2	0.00073527	0.41	0.668
	Mesh × days	6	0.06463569	35.68	<0.001
	Litter × days	3	0.00326835	1.80	0.158
	Litter × mesh × days	5	0.00812670	4.49	0.002
	Error	52	0.00181149		
	Total	81			
C N ratio	Block	7	0.00340369	2.23	0.046
	Litter	1	0.80654274	529.49	<0.001
	Mesh	2	0.21257916	139.56	<0.001
	Days	3	0.01948892	12.79	<0.001
	Litter × mesh	2	0.00158361	1.04	0.361
	Mesh × days	6	0.05688777	37.35	<0.001
	Litter × days	3	0.00328806	2.16	0.104
	Litter × mesh × days	5	0.00735089	4.83	0.001
	Error	52	0.00152324		
	Total	81			

Table 5. Summary of two-way ANOVAs (mesh size and days exposed) of nutrient content of herb spp. litter over 10 weeks of exposure. Pattern of change over time is based upon comparisons of differences between sampling dates by the Least Significant Means (LMS) test

Herb species	Nutrient	Probabilities of *F*'s from two-way ANOVA			Pattern of change over time[a]		
		Mesh	Days	Mesh × Days	Fine mesh	Medium mesh	Coarse mesh
Anemone	Carbon	<0.001	<0.05	<0.001	↑↑	0	↓
	Nitrogen	<0.001	<0.05	<0.001	↑↑	↓	↓↓
	C/N	<0.001	<0.05	<0.001	↓↓	↑	↑↑
Mercurialis	Carbon	NS ($P = 0.11$)	NS ($P = 0.13$)	NS ($P = 0.23$)	↑	↑↓	0
	Nitrogen	<0.001	<0.001	<0.001	↑	↑↓	↓↓
	C/N	<0.001	<0.001	<0.001	↓	↓↑	↑↑

[a] ↑↑ = continual change, with >1 statistically significant difference between dates. ↑ = change, but not continual or less consistent (probably due to few replicates in some cases). ↑↓ = significant increase and decrease. 0 = no statistically significant change

Excluding the fauna clearly affected patterns of change in C, N and C/N of both understory herbs. Effects were most pronounced for *Anemone*. When animals had access to the litter, C and N content decreased, or did not change, instead of increasing; and the C/N ratio increased. The pattern for *Mercurialis* litter is somewhat similar, though more complicated and not as pronounced as for *Anemone*. Carbon and nitrogen increased in the fine-mesh bags, but increases were not as pronounced as for *Anemone*. For *Mercurialis* in medium-mesh bags, percentages of carbon and nitrogen initially increased, but then declined, yielding no net change. The reversal of the pattern was more pronounced when all the fauna had access to *Mercurialis* litter, resembling the shift exhibited by *Anemone*.

Changes in C, N and C/N: canopy species

In order to overcome problems introduced by highly heterogeneous variances, we utilized three approaches to analyzing nutrient content of canopy litter. Because conditions of ANOVA are not satisfied for either the full design or final values, inferences about temporal changes in nutrient content are best made by direct examination of temporal plots of C, N and C/N (Figs. 7–9). Conclusions about impacts of the fauna and differences between categories of litter are based upon the results of two types of ANOVAs of mean values calculated over all sampling dates: (1) two-way ANOVA (litter type × mesh size; Table 6); and one-way ANOVAs of the effect of a particular treatment at each level of the other treatment (Table 7). Separate one-way ANOVAs were necessary because of significant interaction terms in the two-way analyses. Below are the conclusions that emerge from a synthesis of these three approaches.

Categories of canopy litter clearly differed in nitrogen content, with the ash-maple mixture having the highest and fresh beech the lowest. Levels of nitrogen in ash-maple litter were intermediate between those for *Anemone* and *Mercurialis*. Values of % C did not differ substantially between categories of canopy litter, though C content of ash-maple was slightly lower than that of the two types of beech litter (marginally significant differences). Carbon content of all categories of canopy litter was higher than the herbaceous species. C/N values

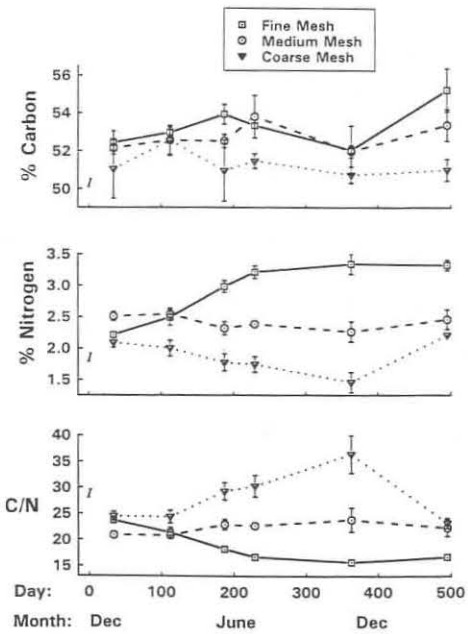

Fig. 7. Change in % C, % N and C/N ratio of ash-maple litter. "*I*" indicates initial values. Means ± SE

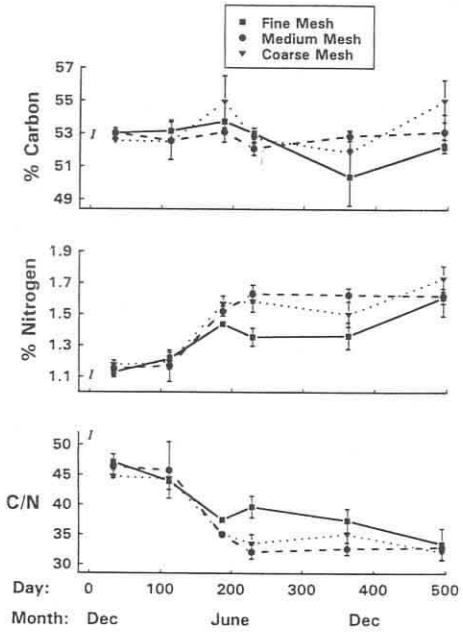

Fig. 8. Change in % C, % N and C/N ratio of freshly fallen beech litter. "*I*" indicates initial values. Means ± SE

reflected differences in nitrogen content, i.e. freshly fallen beech had the highest, ash-maple the lowest. Values of C/N for the ash-maple mixture were similar to those of *Anemone*. Carbon content of all three categories of canopy litter remained fairly constant, with a slight increase after a year. Nitrogen content of both categories of beech litter increased more markedly, leading to parallel declines in C/N. After 1.4 years, N content and C/N ratio of freshly fallen beech were similar to values for aged beech at the start of the experiment, suggesting that the aged beech leaves used for the study had fallen the previous year. The

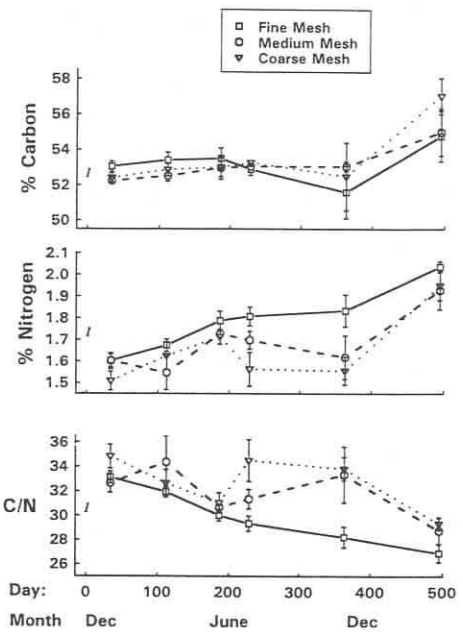

Fig. 9. Change in % C, % N and C/N ratio of aged beech litter. "*I*" indicates intitial values. Means ± SE

Table 6. Summary of two-way ANOVAs (litter type and mesh size) of nutrient content of canopy litter averaged over the entire experiment. Total degrees of freedom are less than the full design because not all replicates were analyzed for nutrient content

Dependent variable	Source of variation	df	MS	*F*	*P*
Carbon	Block	5	1.24850	1.22	0.318
	Litter	2	3.20906	3.13	0.054
	Mesh	2	0.94642	0.92	0.405
	Litter × mesh	4	4.34208	4.24	0.006
	Error	40	1.02419		
	Total	53			
Nitrogen	Block	5	0.01004	0.68	0.644
	Litter	2	4.53243	305.00	<0.001
	Mesh	2	0.82132	55.27	<0.001
	Litter × mesh	4	0.79085	53.22	<0.001
	Error	40	0.01486		
	Total	53			
C/N ratio	Block	5	3.83394	1.33	0.271
	Litter	2	928.14934	322.05	<0.001
	Mesh	2	73.21916	25.41	<0.001
	Litter × mesh	4	81.17158	28.17	<0.001
	Error	40			
	Total	53			

Table 7. Summary of one-way ANOVAs of nutrient content of canopy litter and LSM tests of significant differences between levels of a treatment (litter type or mesh size)

Treatment analyzed by one-way ANOVA	Category within which ANOVA is performed	Response Variable	*P*(*F*)	Results of LMS tests[a, b, c, d]
Litter	Fine mesh	C	NS ($P = 0.31$)	AM = AgB = FrB
		N	<0.001	AM ⋙ AgB ⋙ FrB
		C/N	<0.001	FrB ⋙ AgB ⋙ AM
	Medium mesh	C	NS ($P = 0.57$)	AgB = FrB = AM
		N	<0.001	AM ⋙ AgB > FrB
		C/N	<0.001	FrB ⋙ AgB ⋙ AM
	Coarse mesh	C	<0.05	(FrB = AgB) ⋙ AM
		N	<0.001	AM > AgB > FrB
		C/N	<0.001	FrB ⋙ AgB ⋙ AM
Mesh size	Ash-Maple	C	<0.05	FI = ME > CO
		N	<0.001	FI ⋙ ME ⋙ CO
		C/N	<0.001	CO ⋙ ME ⋙ FI
	Fresh Beech	C	NS ($P = 0.34$)	CO = ME = FI
		N	<0.05	(ME = CO) > FI
		C/N	<0.05	FI ⋙ (CO = ME)
	Aged Beech	C	NS ($P = 0.91$)	CO = ME = FI
		N	<0.01	FI > ME = CO
		C/N	<0.01	CO = ME > FI

[a] AM = ash-maple; FrB = fresh beech; AgB = aged beech; FI = fine mesh; ME = medium mesh; CO = coarse mesh

[b] Values are listed from largest to smallest value, left to right

[c] "$x > y$" signifies that y is less than x with $P < 0.05$; "⋙" signifies $P < 0.01$, etc.; because of the number of comparisons, $P < 0.05$ should only be considered marginally statistically significant

[d] "$(x = y) > z$" signifies that $x > z$ and $y > z$; $x > y > z$ signifies that $x \ggg z$ and $y > z$

pattern of change in nitrogen content of ash-maple is more complicated. Nitrogen in the fine-mesh bags increased over the span of a year; in contrast, N content of the ash-maple mixture did not change in medium-mesh bags, and declined in bags exposed to all faunal categories during the first year of exposure.

The fauna clearly affected the nutrient content of all three categories of canopy litter, but the patterns for each category differed markedly. The overall effects of the fauna on nitrogen and C/N of ash-maple litter were similar to those for the two herb species; even the pattern for effects on carbon content were somewhat similar. In contrast, impact of the fauna on the nutrient content of beech leaves was quite different from that on the ash-maple litter. Excluding fauna had no consistent overall effect on C over the experiment (Table 6), though after 1.4 years carbon content did appear to be higher in the coarse-mesh bags. Carbon content of ash-maple litter in the coarse-mesh bags was lower than all other eight treatment combinations [LSM test within two-way ANOVA (Table 6)]; none of the other treatments differed significantly from each other in C. The fauna had a clearer impact upon nitrogen content (with consequent effects upon C N ratio), but two features distinguish the pattern from that for ash-maple and the herb species: (1) differences between medium- and coarse-mesh bags were not different for either category of beech litter; and (2) exposure to the fauna led to a slight increase, rather than a decrease, in % N of newly fallen beech leaves. This treatment effect, however, is marginally statistically significant, and should be interpreted cautiously. For aged beech leaves the effect was clearer, and was opposite, i.e. similar to that for ash-maple and the herb species.

Discussion

Experimental design

Use of litterbags to investigate factors that influence litter decomposition has a long history (Swift et al. 1979). Inferences from litterbag experiments rest on several assumptions: (1) rates of disappearance of litter are correlated with rates of actual decomposition; (2) the microenvironment within the litter bag is similar to that of the natural litter layer; (3) the litterbags do not substantially interfere with colonization of the litter by the microflora; and (4) mesh differences selectively screen access of the fauna to the litter in a known manner, and with minimal alteration of normal feeding behaviours. Recognizing that these assumptions are not completely satisfied, investigators have studied rates of decomposition by following the disappearance of individually tethered leaves (Witkamp & Olson 1963), by using containers in which the physical arrangement of the litter more closely resembles the natural situation (Herlitzius 1983; Joergensen 1991), and by applying chemicals to reduce densities of selected faunal categories (Seastedt & Crossley 1983; Blair et al. 1992). Although these alternative approaches have proven valuable, the classical litterbag experiment still can provide answers to important questions about the decomposition process (Melillo et al. 1982; Seastedt 1984; Staaf 1987; Blair et al. 1990; Slapokas & Granhall 1991; Wolters 1991). An advantage of the litterbag technique is the relative ease with which large numbers of replicated treatments can be established. The design of our litterbags, the amount of litter we added and our sampling procedures are similar to other studies, allowing us to compare findings directly.

We designed our studies as factorial experiments so that we could use ANOVA to compare effects of litter quality and the fauna on response variables, yet we scheduled treatments so as to reflect the normal phenology of the decomposition process. Because a primary goal was to compare decomposition rates and changes in nutrient content under conditions that were as natural as possible, we placed the leaves on the forest floor at the time they normally fall, rather than holding some of the litter until all species and categories could be placed in the forest simultaneously. Thus, in comparing rates of disappearance of *Anemone* and *Mercurialis*, we have to recognize that differences may reflect not only differences in litter quality,

but also different environmental conditions (*Mercurialis* was exposed 10 weeks later in the season that *Anemone*). Bags of canopy litter were placed on the forest floor three months later than bags of *Mercurialis*. Whenever possible, we have reduced problems of interpretation resulting from different dates of initiation of the experiments by comparing patterns over a full year.

Comparisons with findings of other litterbag experiments

Our experiments reveal that rates of disappearance of understory herb litter exceed those of beech litter by an order of magnitude or more. In addition, our experiments demonstrate clear impacts of the fauna on disappearance rates and changes in nutrient content of the litter during decomposition, but effects vary for different categories of litter. Below we discuss our findings in the context of other studies, pointing out where our results confirm previously documented patterns as well as highlighting new findings or results that differ from other investigations of similar forests.

High rates of disappearance of herb litter. The rapidity with which litter of *Anemone* and *Mercurialis* disappeared in all three types of litterbags is consistent with rates reported by other investigators for herb litter (Bell 1974). It is clear that several elements of the fauna feed heavily on herb litter. *Mercurialis* is fed upon readily by *Lumbricus terrestris* (Satchell 1967), which is the dominant macrofaunal species in the Göttinger Wald (Schaefer 1990).

Slow rate of disappearance of beech litter. Previous research has revealed that among canopy species, beech trees produce litter that is among the slowest to decompose (Heath & Arnold 1966; Heath et al. 1966; Edwards & Heath 1975). Our experiments revealed that litter of ash and maple decomposes much faster than beech, a result consistent with other findings (Heath et al. 1966; Melillo et al. 1982). Differences in decomposition rates between different canopy species, and between canopy and herb litter, likely are caused by different levels of secondary compounds and structural chemicals (Edwards & Heath 1975), and by differing initial concentrations of nutrients, particularly nitrogen (Williams & Gray 1974; Jensen 1974; Hunt 1977; Swift et al. 1979; Vogt et al. 1986). We did not collect data relevant to the first explanation, but our results are consistent with the importance of nitrogen content. Freshly fallen beech had the lowest % N and the slowest rate of decomposition; Aged beech, with higher N, decomposed more rapidly; and *Mercurialis* litter, with the highest % N, disappeared the fastest. Decomposition rates and initial % N were positively correlated for litter protected from, and also exposed to, the fauna [$r(k, \%\ N) = 0.67$ and 0.63 for fine- and coarse-mesh bags, respectively; initial N for *Mercurialis* estimated from Fig. 6]. Also, k and C N were negatively related ($r = -0.71$ and -0.69 for fine and coarse meshes, respectively). None of the correlations, however, is statistically significant (df = 3). With only five types of litter, the power of these tests is low. Small sample size is not the only reason we did not observe a stronger dependence upon N content. *Anemone* had a lower N content than the ash-maple mixture, yet disappeared at a much faster rate; this difference is particularly dramatic for the coarse-mesh bags. Thus factors in addition to N content must also be important for the litter we studied, both with respect to susceptibility to attack by the microflora and palatability to the fauna.

Influence of the fauna on litter decomposition. Our results are generally consistent with previously documented effects of the fauna on rates of disappearance of leaf litter in deciduous forests (Swift et al. 1979). Faunal effects were most pronounced for leaves of herbs, and maple – litter higher in N content. In our study the annual decomposition rates (k) of beech and ash-maple litter that was exposed to the fauna are higher than those found by Melillo et al. (1982; 0.33 versus 0.08 for beech, and 1.81 versus *ca.* 0.45 for ash-maple). Rates of disappearance of beech litter in our study are also greater than those found by Edwards & Heath (1975), but are somewhat lower than those obtained in other studies in the Göttinger Wald (Herlitzius & Herlitzius 1977; Herlitzius 1983; Schaefer 1990).

Relative impact of meso- and macrofauna on patterns of decomposition. Our experiments revealed that both elements of the fauna accelerated the rate of disappearance of litter of herbs, ash and maple. Other studies have also shown that both meso- and macrofauna accelerate decomposition of a variety of litter types (Swift et al. 1979). In contrast, neither element of the fauna affected the rate of disappearance of freshly fallen beech litter, and only the macrofauna consumed aged beech litter. Herlitzius (1983) also found that the fauna did not accelerate the decomposition of fresh beech leaves in the Göttinger Wald.

Changes in nutrient content of the litter during decomposition. Nitrogen content of the litter frequently increases during decomposition (Gosz et al. 1973; Aber & Melillo 1980; Blair 1988). In our study nitrogen content increased, and the C/N ratio decreased, in all five litter types in the fine-mesh bags. This pattern likely reflects a decrease in C due to microbial respiration and an increase in N due to the incorporation of N-rich microbial biomass (Swift et al. 1979). Most litter exposed to the fauna showed an opposite pattern, which N either decreasing or not changing, and C/N increasing or remaining relatively constant. The only exception was the N content of fresh beech litter, which increased slightly when exposed to the fauna. Effects of the fauna on nutrient content were most pronounced for the herbaceous species and the ash-maple mixture, i.e. the litter categories in which the fauna fed most heavily. Faunal effects were less pronounced for aged beech litter, and were absent or very minor for fresh leaf litter, which was largely ignored by the fauna. Relative effects of the meso- and macrofauna on nitrogen content closely mirrored the effects of each faunal category on rates of litter disappearance, suggesting that the nitrogen content of the litter influenced the palatability of the litter to both meso- and macrofauna. The decrease in nitrogen content and increase in C/N ratio of litter exposed to detritivores and fungivores is most readily explained by the selective removal of N-rich litter and associated microflora.

In contrast to our findings, Melillo et al. (1982) found that N content increased over 12 months in ash and maple litter placed in nylon bags with openings comparable to our coarse-mesh bags. Parallel to our results, their beech litter also increased in % N. Although initial % N of beech in their study was similar to our fresh beech litter (0.9% and 1.1%, respectively), N content of their ash and maple litter was lower than beech (< 50% the N content of our ash-maple mixture). This difference, in addition to possible differences in composition of the fauna, may explain the discrepancy between our results and theirs, particularly since they found that decomposition rate was not correlated with initial N content, but was related to the ratio of initial lignin to initial nitrogen. In addition, fauna in their system consumed canopy litter at a slower rate than did animals in the Göttinger Wald.

Consumption of beech litter by the fauna: a complex pattern. It is clear from our experiments and those of other investigators that beech litter is more resistant to decomposition than the litter of other canopy species and understory herbs. Less clear is the extent to which macrofaunal species accelerate the decomposition of beech leaves. No simple pattern emerges with regard to the relative palatability of beech leaves to elements of the macrofauna. On a rich mull site, Staaf (1987) found that 88% of the beech leaves disappeared from 6-mm mesh bags within a year, and 57% from bags exposed solely to the mesofauna. Comparable disappearance rates from our experiments were much lower: 32% and 24%, respectively; and these rates did not differ significantly from the rate of disappearance from our 45 µm-mesh bags. Staff (1987) points to several earlier studies which also demonstrated that excluding the macrofauna decreased the rate of disappearance of beech leaves from litterbags (Heath & Arnold 1966; Anderson 1973; Herlitzius & Herlitzius 1977). A recent experiment in the Göttinger Wald (Joergensen 1991) revealed that access to the macrofauna in litter cages accelerated the rate of disappearance of freshly fallen beech leaves; k's averaged over 2 years for decline in total C per litter container were 0.28 and 0.68 for 1-mm and 12-mm mesh openings, respectively. These values compare with respective values of k for change in litter dry weight in our study of 0.29 and 0.33 for 1-mm and 3.5-mesh ~~mesh~~ bags.

Joergensen's estimate of k agrees with an estimate of $k = 0.8$ calculated from the ratio of litter standing crop to litter fall for the Göttinger Wald (Schaefer 1990). In contrast to Joergensen's findings and in agreement with our results, excluding the macrofauna did not appreciably alter the disappearance rate of beech leaves in another Göttinger Wald experiment (Herlitzius 1983). Herlitzius observed a positive effect of the macrofauna when he added pulverized hay or spruce needles to the beech litter, but the macrofauna did not significantly influence the decomposition of non-amended beech litter. Similar inconsistencies appear in results of experiments in an English forest. In an experiment conducted in an oak-dominant woodland at Rothamsted Experimental Station, beech leaves in 1.5-mm and 7-mm mesh bags that were buried 2.5 cm below the leaf layer decomposed at similar rates, with 95% of the material remaining after 2.5 yrs (Edwards & Heath 1975). In contrast, an earlier study in the same forest revealed higher rates of disappearance of beech leaves that were exposed to the macrofauna in 7-mm bags (ca. 50% disappeared within a year).
The inconsistent pattern that emerges from these studies has several possible explanations: 1) differing accessibility to the macrofauna (mesh sizes of bags permitting entrance of the macrofauna varied from 3.5 – 12 mm); 2) different microclimates within different types of litter containers; 3) differences between forests in composition of the microflora and fauna; 4) different abiotic limiting factors; 5) differences in palatability to the fauna of beech litter from different forests or from the same forest in different years.

Role of herbaceous litter in maintaining high faunal densities in forests on mull soils

Because the fauna contributes significantly to rates of litter disappearance, but consumes different types of litter at different rates, it follows that the overall mixture of litter types throughout the year could determine overall decomposition rate in a non-additive manner. It has been hypothesized that nutrient-rich litter may contribute to higher decomposition rates of more resistant litter (Seastedt 1984). This may also apply to low-quality litter such as beech leaves. Litterbag experiments have demonstrated non-additive effects of litter mixtures on nitrogen fluxes (Blair et al. 1990). Such an interaction between different categories of litter may be particularly important for deciduous forests on mull soils, in which the impact of the fauna on decomposition is particularly strong.
Continuous input during most of the growing season of high quality non-beech litter may be one factor that sustains the high biomass of saprophagous macrofauna (lumbricids, gastropods, diplopods and isopods) that is responsible for the rapid decomposition of litter in many beech forests on mull soils (Schaefer 1990). The dramatic difference in our experiments between rates of utilization by the fauna of beech litter and other litter species supports this hypothesis. In the Göttinger Wald the litter standing crop is primarily beech, but the rate of input of non-canopy leaf litter is substantial (Pellinen 1986; Dierschke 1989; Eggert 1989; Schmidt et al. 1989). The annual input of canopy leaf litter is 331 g m^{-2} yr^{-1}, of which ash-maple constitutes only 5%. Although there are no direct measurements of herb litter input in the Göttinger Wald, Schaefer (1990) was able to estimate from values of NPP that the energy added by herbs to the floor of this forest is nearly one-third of the amount in canopy leaf fall. Thus litter of herbaceous species constitutes a substantial portion of the total energy input, and also is a form of energy much more accessible to the fauna than beech litter. In our experiments only aged beech leaves were consumed by the macrofauna to a significant extent. Hence a forest floor consisting entirely of beech leaves would likely not support nearly as many animals of the macrofauna as would a mixture of beech and edible herb species. Although the physical characteristics of mull soils favor population growth of many faunal species, the continuous input of high-quality herb litter may also be a major factor that sustains animal populations at densities high enough to dramatically accelerate rates of beech decomposition. Our data on relative rates of disappearance of herbaceous and beech litter in the Göttinger Wald support this hypothesis.

Not all studies support this hypothesis to the extent that our findings do. Staaf (1987) argues that *Mercurialis perennis*, which is a preferred food of litter-burying earthworms, is not abundant enough on his site to support even a small fraction of the earthworm population. He postulates that soil pH favors high earthworms' populations on his rich mull site, which leads to high consumption rates of beech litter. It is undoubtedly true that several factors interact to influence macrofaunal densities. Even so, the discrepancies between results of different studies may largely reflect the complex, non-additive manner in which herb litter affects decomposition.

An intimate association of herb and beech leaf litter may be a necessary condition for higher rates of utilization of beech leaves by the fauna. Most litterbag studies have not been designed to test this type of interaction, because they have examined rates of disappearance of homogeneous collection of leaves. Fresh beech leaves might have been consumed at a faster rate in our experiment if they had been mixed with leaves of herb species in the litter bags.

The results of our experiments and the variable patterns of findings from other research strongly suggest it would be worthwhile to continue investigating the factors that maintain high faunal densities in forests on mull soil. In particular, it would be enlightening to conduct long-term manipulations of litter composition in forests with high inputs of herbaceous litter.

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References

Aber, J. D., Melillo, J. M. (1980) Litter decomposition: measuring state of decay and percent transfer into forest soils. Can. J. Bot. **58**, 416–421.

Anderson, J. M. (1973) The breakdown and decomposition of Sweet Chestnut (*Castanea sativa* Mill.) and beech (*Fagus sylvatica* L.) leaf litter in two deciduous woodland soils: I. Breakdown, leaching and decomposition. Oecologia **12**, 251–274.

Bell, M. K. (1974) Decomposition of herbaceous litter. In: Dickinson, C. H., Pugh, G. J. F. (eds.) Biology of plant litter decomposition. Acedemic Press, London, New York.

Blair, J. M. (1988) Nitrogen, phosphorus and sulfur dynamics in decomposing deciduous leaf litter in the southern Appalachians. Soil Biol. Biochem. **20**, 693–701.

Blair, J. M., Parmelee, R. W., Beare, M. H. (1990) Decay rates, nitrogen fluxes, and decomposer communities of single- and mixed-species foliar litter. Ecology **71**, 1976–1985.

Blair, J. M., Crossley, D. A. J., Callaham, L. C. (1992) Effects of litter quality and microarthropods on N dynamics and retention of exogenous ^{15}N in decomposing litter. Biol. Fertil. Soils **12**, 241–252.

Dierschke, H. (1989) Kleinräumige Vegetationsstruktur und phänologischer Rhythmus eines Kalkbuchenwaldes. Verh. Ges. Ökol. **17**, 131–143.

Dierschke, H., Song, Y. (1982) Vegetationsgliederung und kleinräumige Horizontalstruktur eines submontanen Kalkbuchenwaldes. In: Dierschke, H. (ed.) Struktur und Dynamik von Wäldern. Cramer, Vaduz.

Edwards, C. A., Heath, G. W. (1975) Studies in leaf litter breakdown. III. The influence of leaf age. Pedobiologia **15**, 348–354.

Edwards, N. T., Shugart, H. H., McLaughlin, S. B., Harris, W. F., Reichle, D. E. (1981) Carbon metabolism in terrestrial ecosystems. In: Reichle, D. E. (ed.) Dynamic properties of forest ecosystems. Cambridge University Press, Cambridge, UK.
Eggert, A. (1986) Zur Ökologie der Krautschichtvegetation in einem Bärlauch-Kalkbuchenwald. Thesis Göttingen.
Eggert, A. (1989) Zur saisonalen Kohlenstoff- und Stickstoffdynamik der Krautschichtvegetation eines submontanen Kalkbuchenwaldes. Verh. Ges. Ökol. **17**, 167–176.
Ellenberg, H., Mayer, R., Schauermann, J. (1986) Ökosystemforschung. Ergebnisse des Sollingprojektes 1966–1986. Eugen Ulmer, Stuttgart.
Esser, W. (1958) Beitrag zur Untersuchung der Äsung des Rehwildes. Z. Jagdwiss. **4**, 1–40.
Gosz, J. R., Likens, G. E., Bormann, F. H. (1973) Nutrient release from decomposing leaf and branch litter in the Hubbard Brook Forest, New Hampshire. Ecol. Monogr. **43**, 173–191.
Heath, G. W., Arnold, M. K. (1966) Studies in leaf-litter breakdown. II. Breakdown of "sun" and "shade" leaves. Pedobiologia **6**, 238–243.
Heath, G. W., Arnold, M. K., Edwards, C. A. (1966) Studies in leaf litter breakdown. I. Breakdown rates of leaves of different species. Pedobiologia **6**, 1–12.
Herlitzius, H. (1983) Biological decomposition efficiency in different woodland soils. Oecologia **57**, 78–97.
Herlitzius, R., Herlitzius, H. (1977) Streuabbau in Laubwäldern. Untersuchungen in Kalk- und Sauerhumusbuchenwäldern. Oecologia **30**, 147–171.
Howard, P. J. A., Howard, D. M. (1974) Microbial decomposition of tree and shrub leaf litter. Oikos **25**, 341–352.
Hunt, H. W. (1977) A simulation model for decomposition in grasslands. Ecology **50**, 874–877.
Jensen, V. (1974) Decomposition of angiosperm tree leaf litter. In: Dickinson, C. H., Pugh, G. J. F. (eds.) Biology of plant litter decomposition. Academic Press, London, New York.
Joergensen, R. G. (1991) Organic matter and nutrient dynamics of the litter layer on a forest Rendzina under beech. Biol. Fertil. Soils **11**, 163–169.
McClaugherty, C. A., Pastor, J., Aber, J. D., Melillo, J. M. (1985) Forest litter decomposition in relation to soil nitrogen dynamics and litter quality. Ecology **66**, 266–275.
Meentemeyer, V. (1978) Macroclimate and lignin control of litter decomposition rates. Ecology **59**, 465–472.
Meiwes, K. J., Beese, F. (1988) Ergebnisse der Untersuchung des Stoffhaushaltes eines Buchenwaldökosystems auf Kalkgestein. Ber. Forschungszentrum Waldökosysteme B **9**, 1–141.
Melillo, J. M., Aber, J. D., Muratore, J. F. (1982) Nitrogen and lignin control of hardwood leaf litter decomposition dynamics. Ecology **63**, 621–626.
Minderman, G. (1968) Addition, decomposition and accumulation of organic matter in forests. J. Ecol. **56**, 355–362.
Pellinen, P. (1986) Biomasseuntersuchungen im Kalkbuchenwald. Ph. D. Dissertation, Universität Göttingen (Göttingen).
Sah, S. P. (1990) Vergleich des Stoffhaushaltes zweier Buchenwaldökosysteme auf Kalkgestein und auf Buntsandstein. Ber. Forschungszentrum Waldökosysteme A **59**, 1–140.
SAS Institute (1989) SAS user's guide. SAS Inst., Cary, NC.
Satchell, J. E. (1967) Lumbricidae. In: Burges, A., Raw, F. (eds.) Soil Biology. Academic Press, London.
Schaefer, M. (1990) The soil fauna of a beech forest on limestone: trophic structure and energy budget. Oecologia **82**, 128–136.
Schaefer, M., Schauermann, J. (1990) The soil fauna of beech forests: comparison between a mull and a moder soil. Pedobiologia **34**, 299–314.
Schmidt, W., Hartmann, T., Kothe-Heinrich, G., Schultz, R. (1989) Jahresrhythmus und Produktion der Krautschicht in einem Buchenwald. Verh. Ges. Ökol. **17**, 145–157.
Seastedt, T. R. (1984) The role of microarthropods in decomposition and mineralization processes. Ann. Rev. Entomol. **29**, 25–46.
Seastedt, T. R., Crossley, D. A. J. (1983) Nutrients in forest litter treated with naphthalene and simulated throughfall. A field microcosm experiment. Soil Biol. Biochem. **15**, 159–165.
Slapokas, T., Granhall, U. (1991) Decomposition of willow-leaf litter in a short-rotation forest in relation to fungal colonization and palatability for earthworms. Biol. Fertil. Soils **10**, 241–248.
Staaf, H. (1987) Foliage litter turnover and earthworm populations in three beech forests of contrasting soil and vegetation types. Oecologia **72**, 58–64.
Swift, M. J., Heal, O. W., Anderson, J. M. (1979) Decomposition in terrestrial ecosystems. Blackwell Scientific Publishers, Oxford.

Vogt, K. A., Grier, C. C., Vogt, D. J. (1986) Production, turnover, and nutrient dynamics of above- and belowground detritus of world forests. Adv. Ecol. Res. **15**, 303–377.
Wallwork, J. A. (1976) The distribution and diversity of soil fauna. Academic Press, London, New York, San Francisco.
Wieder, R. K., Lang, G. E. (1982) A critique of the analytical methods used in examining decomposition data obtained from litter bags. Ecology **63**, 1636–1642.
Williams, S. T., Gray, T. R. G. (1974) Decomposition of litter on the soil surface. In: Dickinson, C. H., Pugh, G. J. F. (eds.) Biology of plant litter decomposition. Academic Press, London, New York.
Witkamp, M., Olson, J. S. (1963) Breakdown of confined and nonconfined oak litter. Oikos **14**, 138–147.
Wolters, V. (1991) Effects of acid rain on leaf-litter decomposition in a beech forest on calcareous soil. Biol. Fertil. Soils **11**, 151–156.

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